Sexual Dimorphism in the Adult South African (Cape) Fur Seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): Standard Body Length and Skull Morphology

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We examine differences in standard body length and skull morphology of male (n = 65) and female (n = 18) South African (Cape) fur seals, *Arctocephalus pusillus pusillus*, from the coast of southern Africa with the aim to develop an objective method for determining the sex of fur seal skulls. Males were found to be significantly larger than females in standard body length, with K-means cluster analysis successfully identifying 2 relatively homogeneous groups. Principal component analysis (covariance matrix) showed that the underlying data structure for male and female skull variables was different, and that most of this variation was expressed in overall skull size rather than shape. Males were significantly larger than females in 30 of the 31 skull variables. Breadth of brain case was significantly different for the genders. Relative to condylobasal length, males were significantly larger than females in 13 of the 31 skull variables used in the present study. These were gnathion to posterior end of nasals, breadth at preorbital processes, least interorbital constriction, breadth at supraorbital processes, greatest bicanine breadth, breadth of palate at postcanine 1 and 3, calvarial breadth, mastoid breadth, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid and height of mandible at meatus. In males, these variables were associated with the acquisition and defense of territory (e.g.. large head size and mass; increased structural strength of the skull; increased bite capacity). Two skull ratio parameters, breadth of braincase/condylobasal length and length of upper postcanine row/condylobasal length were significantly higher in females compared to males. Based solely on the skull data, mature males can be reliably distinguished from immature males and females using both (a) Classification and Regression Tree (CART) and (b) Hierarchical Cluster Analysis. Both approaches had difficulty in reliably distinguishing immature males from females. The Classification and Regression Tree method was the more successful in correctly distinguishing immature males from females.

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INTRODUCTION

Sexual dimorphism is a form of non-geographic variation that can be generated in a species by the process of sexual selection (Bartholomew, 1970; Alexander et al., 1979; Stirling, 1983). Highly polygynous species such as fur seals, sea lions and elephant seals, generally exhibit a high degree of sexual dimorphism (Laws, 1953; Ralls, 1977; Alexander et al., 1979; Stirling, 1983; Sirianni and Swindler, 1985; McLaren, 1993; Arnould and Warneke, 2002). Differences in reproductive success among males of these species are large, and competition for access to females is intense. Selection pressure appears to favour the development of traits that enhance male fighting ability, including intimidating body size, weaponry and skin thickness (Laws, 1953; Bartholomew, 1970; Le Boeuf, 1974; Alexander et al., 1979; McCann, 1981; Stirling, 1983).

Breeding Southern fur seals *(Arctocephalus* spp.) are among the most territorial of animals, are strongly sexually dimorphic in body size, polygynous and gregarious (Peterson, 1968; Harrison et al., 1968; Stirling, 1970; Bryden, 1972; Alexander et al., 1979; Bonner, 1981; McKenzie et al., 2007). In the southern hemisphere, breeding status male fur seals (beachmasters) generally arrive at the rookeries around November to establish territories. Pregnant females arrive soon after. Once females are present in the male's territory, males guard females until they come into oestrus post-partum. Females give birth within one week of coming ashore and then mate with the nearest male during the short breeding (pupping/ mating) season (Guinet et al., 1998). Males seldom leave the territory until the breeding season is over (Rand, 1967; Stirling, 1970; Miller 1974; Peterson, 1968; Harrison et al., 1968; Bonner, 1981). After mating, the territorial system gradually breaks down and males return to sea to replenish their physiological reserves. Males do not care for their young.

When establishing territories, male fur seals threaten each other with vocal and visual displays, emphasising their size, to intimidate competitors (Bonner, 1968; Stirling, 1970; Stirling and Warneke, 1971; Miller, 1974; Shaughnessy and Ross, 1980). Much time is spent in making visual and vocal threats to rival males and chasing them away, but fights may develop, occasionally resulting in severe injury or death (Rand, 1967; Stirling, 1970; Shaughnessy and Ross, 1980; Trillmich, 1984; Campagna and Le Boeuf, 1988).

Adult male fur seals are about 3 to 5 times heavier and about 1/4 longer than adult females (Stirling, 1983; David, 1989; Boness, 1991; Guinet et al., 1998; Arnould and Warneke, 2002; Stewardson et al., 2009). Large body size is in itself an intimidating form of display to discourage rival males from attempting an actual physical challenge and in the event of a physical challenge is advantageous in competitive interactions and enables breeding bulls to remain resident on territories for longer periods of time without feeding (Rand, 1967; Miller, 1975; Payne, 1978, 1979; Stirling, 1970, 1983). Strong forequarters, enlarged jaw and neck muscles, robust canines, increased structural strength of the skull, and long, thick neck hair (protective mane or wig), also appear to be potentially advantageous in the acquisition and maintenance of territory; quantitative information on these features, however, are lacking (Miller, 1991).

Here we examine morphological differences between skulls (n = 31 variables) of male (n = 65) and female (n = 18) South African (Cape) fur seals *Arctocephalus pusillus pusillus*, from the coast of southern Africa. Body length information was also included in analyses where available. Where possible, comparisons are made to the closely related Australian fur seal *Arctocephalus pusillus doriferus* (King, 1969; Brunner, 1998ab, 2000; Brunner et al., 2002; Arnould and Warneke, 2002; Brunner et al., 2004; Stewardson et al., 2008, 2009) and other otarid species for which morphological data are available such as the Steller sea lion (*Eumetopias jubatus*) (Winship et al., 2001).

For many life history, conservation and ecological studies it is important to be able to determine the sex of skull material in museum collections, skulls of animals found dead or accidentally killed in fishing operations or killed in other ways. Often only the skull is available. We show that two types of multivariate analysis [(a) Classification and Regression Tree (CART) and (b) Hierarchical Cluster Analysis] can be used to objectively distinguish mature male, immature male and female skulls of the South African fur seal (*A. pusillus pusillus*). By extension the approach could be applied to other fur seals, particularly the Australian fur seal (*A. pusillus doriferus*) and the New Zealand fur seal (*A. australis forsteri*).

MATERIALS AND METHODS

Collection of specimens

South African (Cape) fur seals (*Arctocephalus* *pusillus pusillus*) were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S 27° 54'E), from August 1978 to December 1995 (Stewardson et al., 2008, 2009), and accessioned at the Port Elizabeth Museum (PEM). Specimens were collected dead or dying from the coastline and some from accidental drowning in fishnets; none were deliberately killed (cf. Guinet et al., 1998). Routine necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals (1967). Animals were aged from incremental lines observed in the dentine of upper canines (Stewardson et al., 2008, 2009). The sample was supplemented with measurements from 11 known-aged adult males (animals tagged as pups) from Marine and Coastal Management (MCM), Cape Town. The specimens from the MCM collection have accession numbers beginning with MCM (e.g. MCM 1809). The MCM collection also housed 5 tag-aged adult females and 3 tag-aged sub adult/juvenile females.

All animals considered adults had reached full reproductive capacity, i.e., males ≥ 8 y (Stewardson et al., 1998; Stewardson et al., 2008, 2009) and females ≥ 3 y (J.H.M. David, pers. comm.). When age was not known, males ≥ 170 cm (Stewardson et al., 2008, 2009) and females ≥ 135 cm (Guinet et al., 1998; J.H.M. David, pers. comm.) were considered fully adult males and females and included in the analysis as adults even if their dentition age was less than 8 y for males. South African fur seals ≥ 12 y cannot be aged from counts of growth layer groups (GLG) in the dentine of upper canines because of closure of the pulp cavity. Estimated longevity for male South African Fur seals is c. 20 y (Wickens, 1993; Stewardson et al., 2008, 2009). There is much less information on the longevity of female South African fur seals (despite the large numbers of animals that are shot in culling and hunting operations) but Wickens (1993) based on zoo records concluded that females could live to c. 30 y.

Australian male fur seals (*A. pusillus doriferus*) also have a similar lifespan of about 20 years but female Australian fur seals based on age tags are currently known to live to well over 20 y (Arnould and Warneke, 2002). Seal life spans in a range of seal species average about 15 to 20 y for males and in excess of 20 y for females (New Zealand fur seal (*A. australis forsteri*), McKenzie et al., 2007; Antarctic fur seal (*A. gazella*), Payne, 1978, 1979); Steller sea lion (*Eumetopias jubatus*), Winship et al., 2001).

Museum records

The data set on the males used in the present study has already been published in (Stewardson et al., 2008) and further details can be found in Stewardson (2001). The list of male specimens used in the present study is shown in Appendix 1. There were 39 adult males, 24 immature sub adult males and two juvenile males only 2 years old. No standard body length measurements were available on four (4) of the adult males (PEM 2004, PEM 2007, PEM 2013, PEM 2036) but it is unlikely that any adult male skulls would be assigned to the wrong sex because mature male skulls are much larger than females and more heavily built. However, there were no **SBL** measurements available on four (4) of the immature males (PEM 2006, PEM 2009, PEM 2010 and PEM 2014). This raises some doubts about the certainty that these specimens were correctly identified as males. Generally if the **SBL** had been determined, the genitalia would have been available for examination. The raw data set for the females (18 adults, 4 juveniles and sub adults) is shown in Appendix 2 and the means and standard deviations in Appendix 3. All the female carcasses were complete enough for reliable determination of their sex.

Skull variables

A total of 32 skull measurements were recorded (Table 1). However, one of these variables, height of sagittal crest, was not examined statistically because there were few measurements for females and also because we have found that sagittal crest measurements seem to provide little useful information in male skulls (Stewardson et al., 2008). Thus, statistical analysis was conducted on 31 of the 32 variables. Skull preparation and measurement procedures follow Stewardson et al. (2008).

Statistical analyses

Six methods of analyses were employed. Firstly, two sample t-tests (assuming equal variance) were used to test the hypothesis that the mean value of a skull variable was significantly different for males and females against an appropriate alternative hypothesis (H_0: $\mu_{males} = \mu_{females}$; H_1: $\mu_{males} > \mu_{females}$; H_1: $\mu_{females} > \mu_{males}$). Since more than 1 skull variable was being considered, the Bonferroni correction was used - the experiment-wise error rate was divided by the total number of tests performed (Cochran, 1977).

Secondly, K-means clustering, a non-hierarchical cluster analysis was used to classify observations into 1 of 2 groups based on some of the skull variables. Observations on some of the skull variables from both sexes were pooled so that initially there is a single cluster with its centre as the mean vector of the variables considered. These observations were then assigned at random to two sets. Step 1 entails calculating the mean vector of the variables considered (centroid) for each set. Step 2 entails allocating each observation to the cluster whose centroid is closest to that observation. These two steps are repeated until a stopping criterion is met (there is no further change in the assignment of the data points). Before doing this all variables were standardised. Closest neighbour (similarity) was measured using Euclidean distance (Johnson and Wichern, 1992). The groupings of skull variables we considered were dorsal, palatal, lateral and mandibular. We also used k-means clustering to classify observations into 1 of 2 groups using standard body length.

Thirdly, plots of $\log_e$ of each skull variable against $\log_e$ of standard body length (**SBL**) for the genders were examined. 'Robust' regression (Huber M-Regression) was used to fit straight lines ($\log y = \log a + b \log x$) to the transformed data (Weisberg, 1985; Myers, 1990).

Fourthly, principal component analysis (PCA) was used. One useful application of PCA is identifying the most important sources of variation in anatomical measurements for various species (Jackson, 1991; Jolliffe, 2002). When the covariance matrix is used and the data has not been standardized the first principle component (PC) usually has all positive coefficients and according to Jolliffe (2002) this reflects the overall 'size' of the individuals. The other PCs usually contrast some measurements with others and according to Jolliffe (2002) this can often be interpreted as reflecting certain aspects of 'shape', which are important to the species.

Skull measurements were recorded in the same units; therefore a covariance matrix was used to calculate PCs (however this gives greater weight to larger, and hence possibly more variable measurements because the variables are not all treated on an equal footing). Genders were examined separately because the grouped PCA was quite different, in most cases, to either the separate male PCA or female PCA.

PCA and two sample t-tests were calculated in Minitab (Minitab Inc., Slate College, 1999, 12.23). K-means cluster analyses for skull variables and **SBL** were calculated in Minitab (Minitab Inc., Slate College, 1999, 12.23) and in SPSS (SPSS Inc., Chicago, Illinois, 1989-1999, 9.0.1), respectively. This was necessary because Minitab could only perform K-means cluster analysis for 2 or more variables, therefore **SBL** (a single variable) was analysed in SPSS. The regressions were fitted in S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1).

Fifthly, the data mining approach, Classification and Regression Trees (CART), a technique that generates a binary decision tree, was used to classify the observations. In this approach, the set of data is progressively sub-divided based on values of predictor variables into groups that contain higher proportions of "successes" and higher proportions of "failures". The relative importance of the predictor variables is assessed in terms of how much they contribute to successful splits into more homogeneous sub-groups. The classification is most commonly carried out using the Gini criterion, which always selects the split that maximises the proportion of "successes" in one of the groups (Petocz, 2003). Data mining techniques are attractive because no distributional assumptions are needed, data sets can have missing data and analyses are less time consuming. The training data used to create the binary decision set was the set of all animals that have already been determined to be adult males, immature males and mature females. SPSS Clementine 12.0 was used for the analysis.

Finally, Minitab was also used to perform hierarchical clustering and produce dendrograms showing the degree of similarity of the skull data for males, females and immature males. In general, the conclusions reached were similar to those from the CART analysis: it was possible to distinguish mature males from immature males and mature females but it was not possible to clearly distinguish immature males from females.

Unless otherwise stated values are means quoted ± standard errors with the number of data points in brackets.

RESULTS

Standard body length (SBL)

SBL ranged from 157-201 cm in males (n = 33, **SBL** was not recorded for 4 of the adult males) and 135-179 cm in females (n = 18). Mean lengths were 182.9 ± 2.3 (n = 33) and 149.1 ± 2.5 (n = 18), respectively. The two sample t-tests on our data indicated that adult males were significantly larger than adult females (Table 1). The ratio of mean female **SBL** to mean male **SBL** was 1:1.23.

K-means cluster analysis successfully identified 2 relatively homogeneous groups from the pooled data, i.e., cluster 1, predominantly males and cluster 2, predominantly females (Table 2). Of the 18 females, 17 (94%) were correctly classified. Of the 33 males, 28 (85%) were correctly classified.

Table 1: Summary statistics (mean, S.E, C.V. & n) for skull measurements (mm) and standard body lengths (cm) from male and female South African fur seals (*Arctocephalus pusillus pusillus*), and comparison between the mean of the two sexes (two sample t-test). Skull measurements relative to condylobasal length (CBL) are given in brackets. Refer to Stewardson et al. (2008) for a description of skull measurement procedures.

Skull variables	**Male**				**Female**				**Two sample t-test**			**Significant Size Difference**
	mean	**S.E.**	**C.V.**	**n**	**mean**	**S.E.**	**C.V.**	**n**	**T**	**P**	**df**	
Dorsal												
D1 Condylobasal length **(CBL)**	247.1	2.1	5.2	37	212.2	1.8	3.5	18	12.7	< 0.0005	50	**M > F****
D2 Gnathion to middle of occipital crest	217.7 (0.88)	2.8 (0.005)	7.6 (3.43)	35	182.9 (0.86)	1.4 (0.004)	3.2 (2.07)	18	^{T}11.5 (2.64)	< 0.0005 (0.011)	50 (49)	**M > F**** (M = F)
D3 Gnathion to posterior end of nasals	88.9 (0.36)	1.2 (0.003)	8.4 (4.72)	36	72.5 (0.34)	1.0 (0.003)	5.8 (4.26)	18	10.3 (3.96)	< 0.0005 (< 0.0005)	51 (39)	**M > F**** **(M > F**)**
D4 Greatest width of anterior nares	28.6 (0.12)	0.5 (0.001)	9.4 (6.98)	36	24.0 (0.11)	0.5 (0.002)	7.8 (6.87)	15	6.9 (0.96)	< 0.0005 (0.345)	37 (27)	**M > F**** (M = F)
D5 Greatest length of nasals	44.0 (0.18)	0.9 (0.003)	11.7 (8.70)	35	37.5 (0.18)	0.7 (0.003)	7.4 (6.29)	17	5.9 (0.03)	< 0.0005 (0.978)	49 (42)	**M > F**** (M = F)
D6 Breadth at preorbital processes	68.1 (0.28)	0.9 (0.002)	7.4 (4.61)	33	53.3 (0.25)	1.0 (0.003)	6.9 (5.15)	14	^{T}11.2 (5.95)	< 0.0005 (< 0.0005)	33 (24)	**M > F**** **(M > F**)**
D7 Least interorbital constriction	37.7 (0.15)	0.5 (0.002)	7.8 (7.12)	32	28.0 (0.13)	0.9 (0.003)	12.4 (10.45)	16	^{T}9.7 (5.52)	< 0.0005 (< 0.0005)	26 (24)	**M > F**** **(M > F**)**
D8 Breadth at supraorbital processes	56.8 (0.23)	0.9 (0.003)	9.3 (8.35)	33	43.9 (0.21)	1.0 (0.004)	8.9 (7.75)	16	9.6 (4.60)	< 0.0005 (< 0.0005)	38 (35)	M > F** **(M > F**)**
D9 Breadth of brain case	84.2 (0.34)	0.6 (0.003)	4.5 (5.63)	36	82.0 (0.39)	1.1 (0.005)	5.5 (5.09)	18	1.8 (7.87)	0.089 (< 0.0005)	29 (33)	M = F **(F > M**)**
Palatal												
P10 Palatal notch to incisors	105.0 (0.42)	1.4 (0.004)	8.1 (5.12)	37	88.0 (0.41)	1.6 (0.007)	7.9 (6.75)	18	7.9 (1.30)	< 0.0005 (0.204)	40 (27)	**M > F**** (M = F)
P11 Length of upper postcanine row	60.4 (0.24)	0.7 (0.002)	7.4 (6.08)	37	54.9 (0.26)	0.6 (0.003)	4.7 (4.58)	18	5.8 (3.87)	< 0.0005 (< 0.0005)	51 (41)	**M > F**** **(F > M**)**
P12 Greatest bicanine breadth	50.9 (0.21)	0.9 (0.002)	10.1 (6.75)	37	37.0 (0.17)	0.8 (0.003)	9.5 (6.80)	18	11.7 (8.72)	< 0.0005 (< 0.0005)	47 (39)	**M > F**** **(M > F**)**
P13 Gnathion to posterior end of maxilla	116.4 (0.47)	1.2 (0.002)	6.4 (2.82)	36	99.0 (0.47)	0.9 (0.002)	3.8 (1.71)	17	11.4 (1.83)	< 0.0005 (0.740)	50 (47)	**M > F**** (M = F)

Table 1 continued

Skull variables	**Male**				**Female**				**Two sample t-test**			**Significant Size Difference**
	mean	**S.E.**	**C.V.**	**n**	**mean**	**S.E.**	**C.V.**	**n**	**T**	**P**	**df**	
P14 Breadth of zygomatic root of maxilla	15.7 (0.06)	0.3 (0.001)	13.3 (10.19)	37	12.2 (0.06)	0.3 (0.001)	11.0 (10.27)	18	7.6 (3.49)	< 0.0005 (0.001)	48 (36)	M > F** (M = F)
P15 Breadth of palate at postcanine 1	25.7 (0.01)	0.6 (0.002)	13.4 (11.05)	33	18.7 (0.09)	0.5 (0.002)	12.3 (10.39)	18	8.7 (5.32)	< 0.0005 (< 0.0005)	46 (42)	M > F** (M > F**)
P16 Breadth of palate at postcanine 3	27.8 (0.11)	0.5 (0.002)	10.9 (8.74)	34	21.1 (0.10)	0.3 (0.002)	6.7 (6.45)	17	10.8 (5.37)	< 0.0005 (< 0.0005)	48 (45)	M > F** (M > F**)
P17 Breadth of palate at postcanine 5	33.8 (0.14)	0.5 (0.002)	9.7 (7.71)	36	26.8 (0.13)	0.5 (0.002)	8.0 (8.02)	18	9.4 (3.42)	< 0.0005 (0.002)	48 (35)	M > F** (M = F)
P18 Gnathion to hind border of postglenoid process	187.5 (0.76)	1.9 (0.002)	6.1 (1.56)	35	159.0 (0.75)	1.5 (0.003)	4.0 (1.43)	18	11.6 (2.43)	<0.0005 (0.020)	50 (37)	M > F** (M = F)
P19 Bizygomatic breath	141.4 (0.57)	1.7 (0.006)	7.4 (5.88)	37	120.1 (0.57)	1.8 (0.005)	6.5 (4.10)	18	8.5 (0.87)	<0.0005 (0.388)	44 (46)	M > F** (M = F)
P20 Basion to zygomatic root (anterior)	168.5 (0.68)	1.5 (0.002)	5.4 (1.70)	36	145.5 (0.69)	1.2 (0.003)	3.6 (1.62)	18	^{T}11.8 (1.61)	< 0.0005 (0.117)	50 (35)	M> F** (M = F)
P21 Calvarial breadth	116.7 (0.47)	1.1 (0.003)	5.5 (3.20)	35	95.2 (0.45)	1.0 (0.003)	4.5 (2.79)	18	^{T} 14.4 (5.73)	< 0.0005 (< 0.0005)	50 (40)	M> F** (M > F**)
P22 Mastoid breadth	132.6 (0.54)	1.7 (0.004)	7.6 (4.26)	35	107.5 (0.51)	1.4 (0.005)	5.7 (3.80)	18	11.2 (5.13)	< 0.0005 (< 0.0005)	49 (40)	M> F** (M > F**)
P23 Basion to bend of pterygoid	79.0 (0.32)	0.6 (0.002)	4.5 (3.23)	35	69.4 (0.33)	0.7 (0.002)	4.1 (3.10)	18	10.6 (2.29)	< 0.0005 (0.028)	41 (35)	M > F** (M = F)
Lateral												
L24 Gnathion to foramen infraorbital	75.0 (0.30)	0.9 (0.001)	7.0 (3.00)	37	60.8 (0.29)	1.1 (0.004)	7.3 (5.49)	17	10.3 (4.06)	< 0.0005 (0.0006)	36 (21)	M > F** (M > F*)
L25 Gnathion to hind border of preorbital process	82.2 (0.33)	1.0 (0.002)	7.0 (2.87)	36	65.8 (0.31)	0.9 (0.003)	5.2 (3.36)	16	12.8 (6.77)	< 0.0005 (< 0.0005)	45 (26)	M > F** (M > F*)
L26 Height of skull at bottom of mastoid	108.7 (0.49)	1.8 (0.005)	10.0 (6.54)	36	88.7 (0.41)	1.5 (0.004)	5.7 (3.59)	11	8.5 (3.79)	< 0.0005 (0.0006)	37 (33)	M > F** (M > F**)
L27a Height of sagittal crest	-	-	-	-	-	-	-	-	-	.	-	-

Table 1 continued

Mandibular												
M28 Length of mandible	173.7 (0.70)	1.7 (0.002)	5.9 (2.09)	36	146.2 (0.69)	1.9 (0.005)	5.5 (2.75)	17	10.6 (2.20)	< 0.0005 (0.038)	39 (25)	**M > F**** (M = F)
M29 Length of mandibular tooth row	69.9 (0.29)	0.8 (0.002)	6.0 (4.49)	31	55.2 (0.26)	1.5 (0.007)	10.9 (11.19)	17	^{T}10.0 (^{T}3.70)	< 0.0005 (< 0.001)	40 (26)	**M > F**** (M = F)
Skull variables	**Male**				**Female**				**Two sample t-test**			**Significant Size Difference**
	mean	**S.E.**	**C.V.**	**n**	**mean**	**S.E.**	**C.V.**	**n**	**T**	**P**	**df**	
M30 Length of lower postcanine row	47.1 (0.19)	0.4 (0.001)	5.7 (4.55)	35	42.5 (0.20)	0.5 (0.002)	5.0 (4.47)	16	6.6 (3.62)	< 0.0005 (< 0.001)	35 (28)	**M > F**** (M = F)
M31 Height of mandible at meatus	58.3 (0.24)	1.1 (0.003)	11.3 (7.97)	37	44.1 (0.21)	0.9 (0.003)	8.7 (6.64)	17	10.0 (6.10)	< 0.0005 (< 0.0005)	48 (41)	**M > F**** **(M > F**)**
M32 Angularis to coronoideus	58.7 (0.24)	1.0 (0.003)	10.5 (6.70)	35	47.3 (0.22)	0.9 (0.003)	7.4 (6.01)	17	8.4 (3.22)	< 0.0005 (0.0026)	48 (37)	**M > F**** (M = F)
Standard body length (SBL)	182.9	2.3	7.2	33	149.1	2.5	7.1	18	10.0	< 0.0005	41	**(M > F**)**

a Height of sagittal crest (L27) was not examined statistically because there were too few measurements for females. However, in large animals, male crest height was greater than female crest height.

Students-t normality assumption did not hold (data skewed); therefore the data was transformed using Box-Cox transformation (Myers, 1990).

* Significant at the 5% level, with Bonferroni correction.

** Significant at the 1% level, with Bonferroni correction.

df values were calculated for a two sample t-test allowing for unequal variances.

C.V. is coefficient of variation S.E./mean X 100.

Table 2: Classification of skull measurements of South African fur seals using K-means clusters analysis. n is the number of animals. All variables except standard body length (SBL) were standardised (dorsal, palatal and mandibular).

Skull variables	Sex	Cluster 1	Cluster 2	n
Dorsal	Male	22 (96%)	1 (4%)	23
	Female	0	11 (100%)	11
Palatal	Male	24 (92%)	2 (8%)	26
	Female	0	17 (100%)	17
Lateral	Male	28 (80%)	7 (20%)	35
	Female	0	10 (100%)	17
Mandibular	Male	25 (93%)	2 (7%)	27
	Female	1 (6%)	16 (94%)	17
Standard body length	Male	28 (85%)	5 (15%)	33
	Female	1 (6%)	17 (94%)	18

Skull variables

Absolute skull size: two sample t-tests

The two sample t-tests indicated that 30 of the 31 mean skull variables were significantly larger in males than in females, i.e., we reject H_0 in favour of H_1: $\mu_{male} > \mu_{female}$ (Table 1, Fig. 1). Mean value of breadth of brain case **(D9)** was not significantly different for the genders (Table 1). The coefficient of variation (C.V.) was larger in males, with the following exceptions: least interorbital constriction **(D7)**, breadth of brain case **(D9)**, gnathion to anterior of foramen infraorbital **(L24)** and length of mandibular tooth row **(M29)** (Table 1). Height of sagittal crest **(L27)** was not examined statistically because there were too many skulls with missing or damaged sagittal crests.

Relative skull size: two sample t-tests

When skull variables were analysed relative to condylobasal length **(CBL, D1)**, males were found to be significantly larger than females for 13 (43%) variables: (1) gnathion to posterior end of nasals **(D3)**, (2) breadth at preorbital processes **(D8)**, (3) least interorbital constriction **(D7)**, (4) breadth at supraorbital processes **(D8)**, (5) greatest bicanine breadth **(P12)**, (6) breadth of palate at postcanine 1

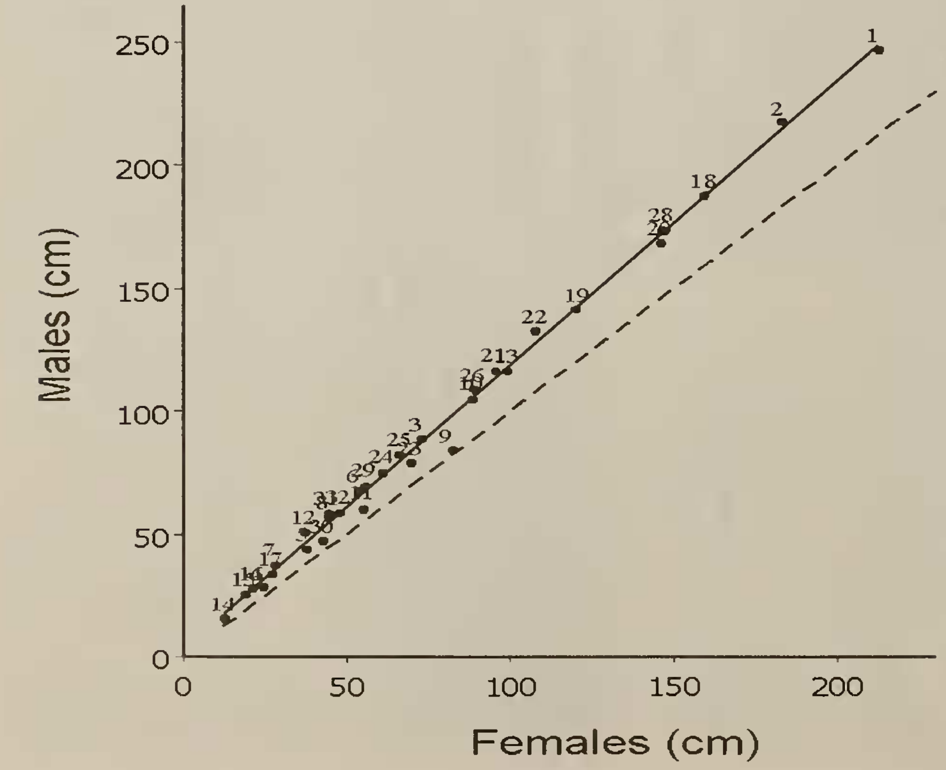


Fig. 1: Mean values of 31 skull variables for male and female South African fur seals. Numbers correspond to skull variables listed in Table 1 (numbers 1-9 correspond to parameters D1 to D9, 10-23 to P10 to P23 and 24-32 to L24 to L32). Numbers above the dashed line, males > females; numbers on the line, males = females; numbers below the line, females > males. Minitab could only perform K-means cluster analysis if there was ≥ 2 variables, therefore SBL (a single variable) was analysed in SPSS. SBL was not recorded for 4 of the 39 males (i.e., n = 35).

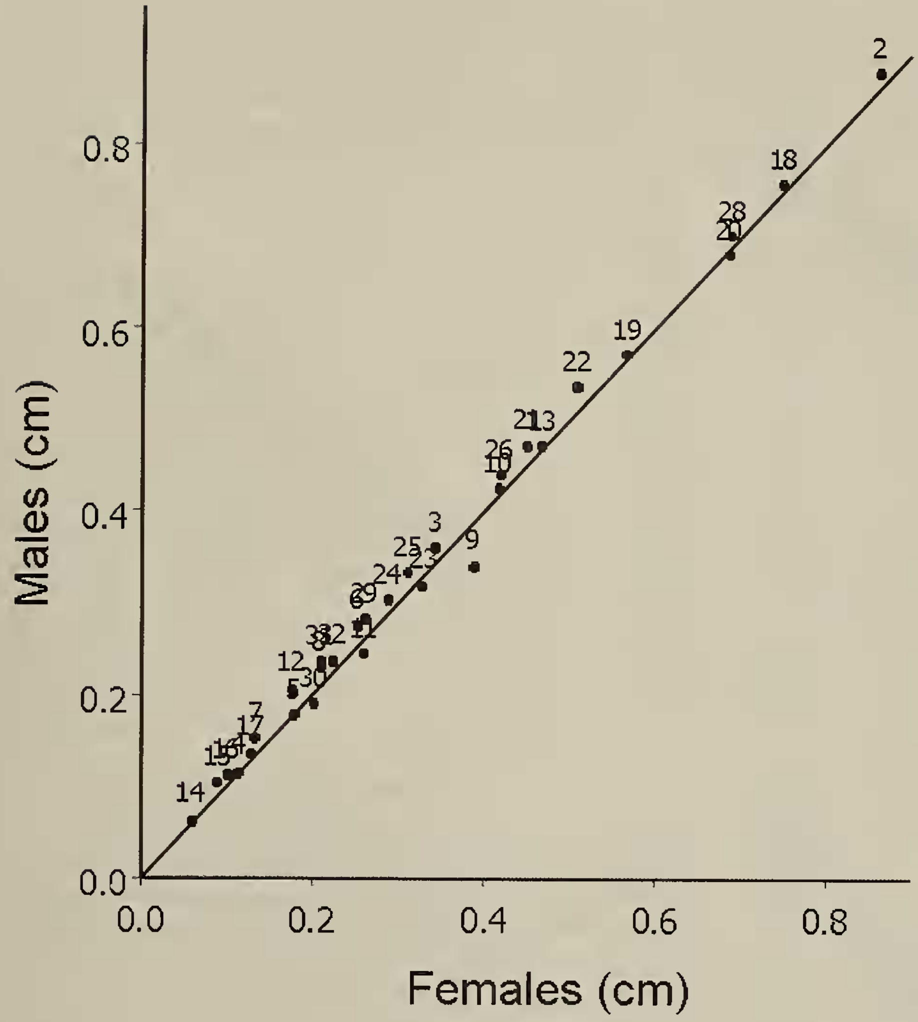


Fig. 2: Mean values of 30 skull variables, relative to condylobasal length, for male and female South African fur seals. Numbers correspond to skull variables listed in Table 1 (numbers 1-9 correspond to parameters D1 to D9, D10-23 to P10 to P23 and P24-32 to L24 to L32). Numbers above the line, males > females; numbers on the line, males = females, numbers below the line, females > males.

(P15), (7) breadth of palate at postcanine 3 **(P16)**, (8) calvarial breadth **(P21)**, (9) mastoid breadth **(P22)**, (10) gnathion to foramen infraorbital **(L24)**, (11) gnathion to hind border of preorbital process **(L25)**, (12) height of skull at bottom of mastoid **(L26)** and (13) height of mandible at meatus **(M31)** (Table 1, Fig. 2). Differences between the genders were highly significant ($P < 0.001$); apart from gnathion to foramen infraorbital **(L24)** and height of skull at bottom of mastoid **(L26)**, which were significant at the 5% level (Table 1).

Breadth of brain case **(D9)** was significantly different in 'absolute size' for males and females, but 'relative to **CBL**' parameter **D9/D1** for females was larger than males (Table 1). Length of upper postcanine row **(P11)** was larger in 'absolute size' in males, but 'relative to **CBL**' **P11/D1** in females was larger than in males (Table 1).

The remaining 15 (50%) variables were not significantly different for the genders (Table 1). Since males were larger than females in 'absolute size', this suggested that the 15 variables were proportionate to **CBL** regardless of sex, i.e., the ratio relative to **CBL (D1)** was significantly different for the genders.

The coefficient of variation for values 'relative to **CBL**' was larger in males for about 1/3 rd of all variables (Table 1). Exceptions were breadth at preorbital processes **(D6)**, least interorbital constriction **(D7)**, palatal notch to incisors **(P10)**, breadth of zygomatic root of maxilla **(P14)**, breadth of palate at postcanine 5 **(P17)**, gnathion to foramen infraorbital **(L24)**, gnathion to hind border of preorbital process **(L25)**, length of mandible **(M28)** and length of mandibular tooth row **(M29)**. The coefficients of 2 of these variables (least interorbital constriction **(D7)** and length of mandibular tooth row **(M29)**) were considerably larger in females in both 'absolute size' and size 'relative to **CBL**' **(M29/D1** and **D7/D1)**.

K-means cluster analysis

K-means cluster analysis successfully identified 2 relatively homogeneous groups from the pooled data, i.e., cluster 1, predominantly males and cluster 2, predominantly females (Table 2). Classification based on dorsal, palatal and mandibular observations was highly successful in recapturing the 2 groups. Classification based on lateral observations was less successful.

Apart from 1 mandibular variable, all females were correctly classified. The majority of males were correctly classified with the following exceptions - 1 dorsal, 2 palatal, 2 mandibular and 7 lateral variables were incorrectly classified as females (Table 2). Misclassification occurred in small males only.

Fig. 3

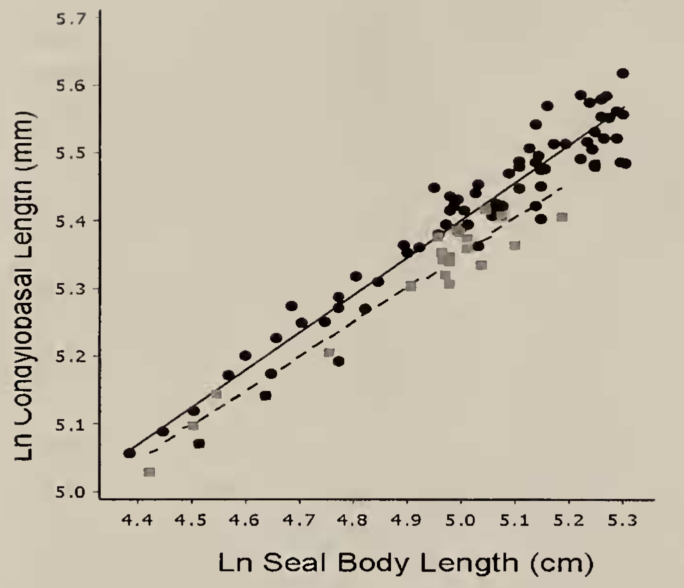


Fig. 5

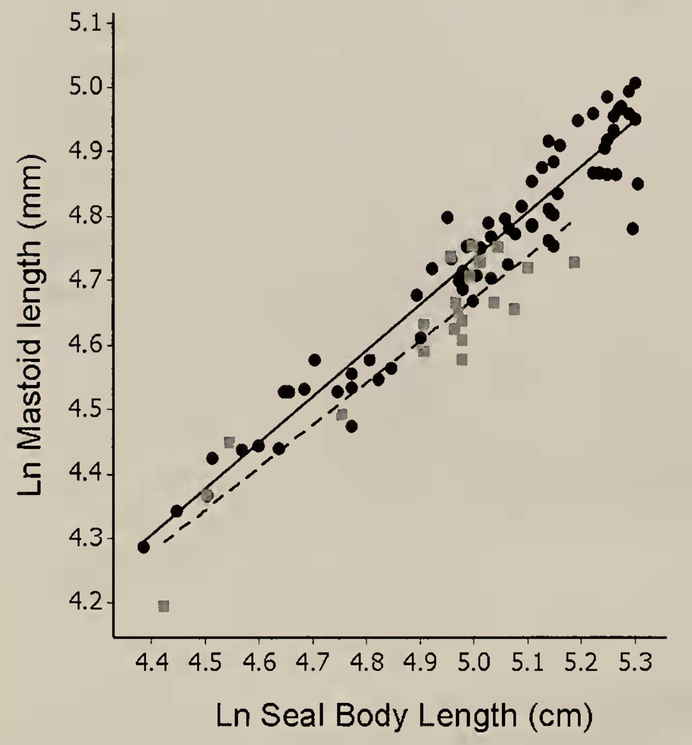
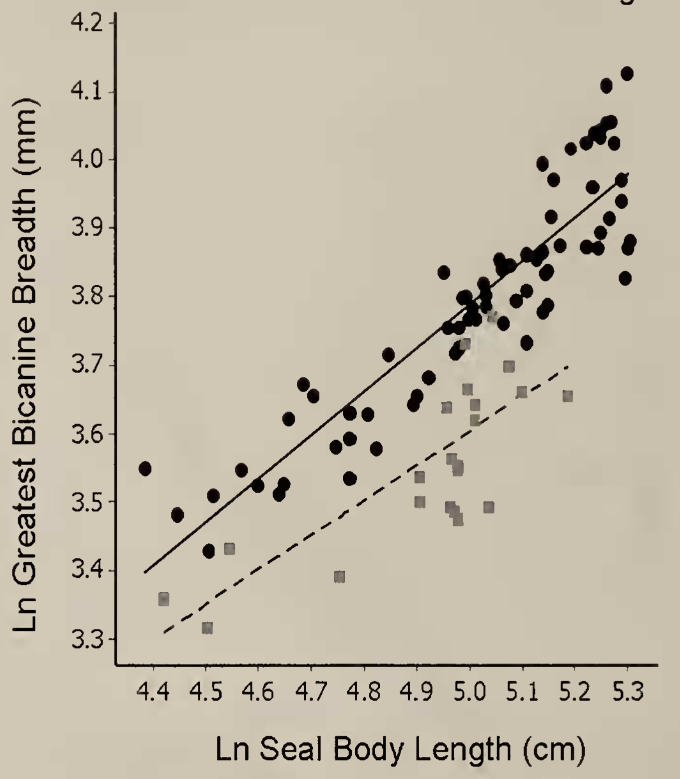


Fig. 4



Figs. 3, 4 & 5: Bivariate plot of: (3) log [CBL (D1) (mm)] on log (SBL (cm)); (4) log [greatest bicanine breadth (P12) (mm)] on log (SBL (cm)); (5) log [mastoid breadth (P22) (mm)] on log (SBL (cm). Circles, males. Squares, females.

Linear regression

All transformed variables were regressed on $\log_e$ (**SBL** in cm). Three variables that best depicted maximum discrimination between the sexes, using regression, are given in Figs. 3, 4 and 5. These were **CBL (D1)**, greatest bicanine breadth **(P12)** and mastoid breadth **(P22)**. These plots (males closed black circles, females grey squares) clearly show pronounced sexual dimorphism in adult South African fur seals, supporting findings of the two-sample t-test and K-means cluster analysis.

Principal component (PC) analysis

The first 3 PCs accounted for most of the variation. The first PC (PCI) can be interpreted as a measure of overall skull size while PC2 and PC3 define certain aspects of shape (Table 3). Interpretations for the first 3 PCs for the 2 genders are given in Table 4, together with the percentage of total variation given by each PC. The variances of corresponding PCs for the two genders do vary and interpretations are dissimilar for most pairs of PCs.

Determining the gender of an isolated skull

It is claimed that it is often possible to make a visual determination of the gender of an isolated South African fur seal skull, provided the skull is from an adult animal (Brunner, 1998ab). However, visual identification based on morphology of the skull alone can be misleading, e.g., young adult males can be mistaken for larger, older females and sex determination of a pup from examining the skull alone would be very difficult. A more objective procedure in determining sexes of skulls would be desirable. In most practical situations if the carcass was available for examination, the sex would usually be determinable, however for many museum specimens only the skull is available. The

Table 3: Principal component (PC) analysis of covariance matrix for adult male and adult female South African fur seals, showing principal components, eigenvalues, proportions and cumulative proportions of the first three principal components. Proportion gives the amount of the total variation that the PC accounted for. Cumulative tally gives the amount the first PC accounted for, then the amount that the first two PCs accounted for and finally the amount of total variation the first three PCs accounted for. Height of sagittal crest (L27) was not examined statistically because there were few measurements for females.

	PC I	PC II	PC III	PC I	PC II	PC III
Dorsal	Males (n = 23)			Females (n = 10)		
D1 Condylobasal length	-0.58	-0.35	-0.50	-0.61	0.48	0.38
D2 Gnathion to middle of occipital crest	-0.71.	-0.06	0.52	-0.28	-0.001	-0.32
D3 Gnathion to posterior end of nasals	-0.28	0.30	-0.28	-0.24	-0.49	0.09
D4 Greatest width of anterior nares	-0.10	0.16	0.03	-0.16	0.28	0.06
D5 Greatest length of nasals	-0.16	0.34	0.02	-0.08	-0.25	0.04
D6 Breadth at preorbital processes	-0.19	0.30	-0.28	-0.41	0.15	-0.17
D7 Least interorbital constriction	-0.08	0.29	0.09	-0.37	-0.15	-0.14
D8 Greatest breadth at supraorbital processes	-0.08	0.49	0.38	-0.36	-0.39	-0.43
D9 Breadth of brain case	-0.03	-0.48	0.41	-0.15	-0.44	0.71
Eigenvalue	**444.9**	**36.1**	**15.7**	**93.7**	**17.7**	**12.7**
Proportion	**0.84**	**0.07**	**0.03**	**0.68**	**0.13**	**0.09**
Cumulative	**0.84**	**0.91**	**0.94**	**0.68**	**0.81**	**0.91**
Palatal	Males (n = 26)			Females (n = 16)		
P10 Palatal notch to incisors	-0.31	-0.21.	0.82	-0.34	0.83	0.32
P11 Length of upper postcanine row	-0.13	-0.13	0.10	-0.08	-0.06	-0.02
P12 Greatest bicanine breadth	-0.19	0.03	-0.01	-0.20	-0.08	-0.19
P13 Gnathion to posterior end of maxilla	-0.30	-0.34	-0.06	-0.24	0.04	0.10
P14 Breadth of zygomatic root of maxilla	-0.07	-0.01	-0.003	-0.03	-0.04	0.04
P15 Breadth of palate at postcanine 1	-0.10	0.03	-0.14	-0.11	0.08	-0.21
P16 Breadth of palate at postcanine 3	-0.08	0.04	-0.08	-0.03	0.09	-0.24
P17 Breadth of palate at postcanine 5	-0.10	0.05	-0.14	-0.02	0.08	-0.24
P18 Gnathion to posterior border of postglenoid	-0.50	-0.18	-0.06	-0.41	-0.16	-0.21
P19 Bizygomatic breadth	-0.30	0.86	0.23	-0.53	-0.15	0.27
P20 Basion to zygomatic root	-0.41	-0.11	-0.13	-0.30	0.13	-0.66
P21 Calvarial breadth	-0.25	0.13	-0.31	-0.26	-0.15	0.19
P22 Mastoid breadth	-0.39	0.05	-0.28	-0.37	-0.42	0.17
P23 Basion to bend of pterygoid	-0.13	-0.08	-0.13	-0.13	0.14	0.26
Eigenvalue	**507.1**	**84.4**	**35.0**	**155.5**	**44.4**	**13.9**
Proportion	**0.73**	**0.12**	**0.05**	**0.62**	**0.18**	**0.06**
Cumulative	**0.73**	**0.85**	**0.90**	**0.62**	**0.79**	**0.85**
Lateral	Males (n = 35)			Females (n = 10)		
L24 Gnathion to anterior of foramen infraorbital	0.39	-0.56	0.73	0.24	-0.71	0.66
L25 Gnathion to posterior border of preorbital process	0.43	-0.59	-0.68	0.33	-0.58	-0.74
L26 Height of skull at base of mastoid	0.82	0.58	0.01	0.91	0.40	0.09
L27a Height of sagittal crest	-	-	-	-	-	-
Eigenvalue	**153.8**	**14.5**	**0.7**	**31.4**	**6.3**	**0.8**
Proportion	**0.91**	**0.09**	**0.004**	**0.82**	**0.16**	**0.02**
Cumulative	**0.91**	**0.996**	**1.00**	**0.82**	**0.98**	**1.00**
Mandibular	Males (n = 26)			Females (n = 16)		
M28 Length of mandible	-0.73	0.38	-0.41	-0.86	-0.20	-0.35
M29 Length of mandibular tooth row	-0.19	0.45	0.57	-0.13	0.96	-0.23
M30 Length of lower postcanine row	-0.12	0.47	0.13	-0.15	-0.09	-0.37
M31 Height of mandible at meatus	-0.49	-0.48	0.63	-0.37	0.05	0.50
M32 Angularis to coronoideus	-0.42	-0.46	-0.31	-0.30	0.14	0.66
Eigenvalue	**145.2**	**13.9**	**8.0**	**88.5**	**27.2**	**9.1**
Proportion	**0.84**	**0.08**	**0.05**	**0.70**	**0.21**	**0.07**
Cumulative	**0.84**	**0.92**	**0.97**	**0.70**	**0.91**	**0.98**

Table 4: Interpretations for the first 3 principal components for the skulls parameters for adult male and adult female South African fur seals. Variables that contributed predominantly to size and/or shapes, i.e. variables with loadings ≥ 0.36 (absolute value) were used in the covariance matrix. Only 2 principal components were considered for the analysis of lateral components because component 3 was 2% or less of total variation.

Male	Female
Dorsal Component 1 (male 84%, female 68%)	
CBL **(D1)** and gnathion to middle of occipital crest **(D2)** measure overall size.	CBL **(D1)**, breadth at preorbital processes **(D6)**, least interorbital constriction **(D7)** and greatest breadth at supraorbital processes **(D8)** measures overall size.
Component 2 (male 7%, female 13%)	
Contrasts greatest breadth at supraorbital processes **(D8)** with CBL **(D1)** and breadth of brain case **(D9)**.	Contrasts CBL **(D1)** with gnathion to posterior end of nasals **(D3)**, greatest breadth at supraorbital processes **(D8)** and breadth of brain case **(D9)**.
Component 3 (male 3%, female 9%)	
Contrasts CBL **(D1)** with gnathion to middle of occipital crest **(D2)**, greatest breath at supraorbital processes **(D8)** and breath of brain case **(D9)**.	Contrasts greatest breadth at supraorbital processes **(D8)** with CBL **(D1)** and breadth of brain case **(D9)**.
Palatal Component 1 (male 73%, female 62%)	
Gnathion to posterior border of postglenoid process **(P18)**, basion to zygomatic root **(P20)** and mastoid breadth **(P22)** measure overall size.	Gnathion to posterior border of postglenoid process **(P18)**, bizygomatic breath **(P19)** and mastoid breadth **(P22)** measure overall size.
Component 2 (male 12%, female 18%)	
Bizygomatic breadth **(P19)** dominates.	Contrasts palatal notch to incisors **(P10)** with mastoid breadth **(P22)**.
Component 3 (male 5%, female 6%)	
Palatal notch to incisors **(P10)** dominates	Bastion to zygomatic root **(P20)** dominates.
Lateral (only 2 PCs considered) Component 1 (male 91%, female 82%)	
Height of skull at base of mastoid **(L26)**, gnathion to posterior border of preorbital process **(L25)** and gnathion to anterior of foramen infraorbital **(L24)** measure overall size.	Height of skull at base of mastoid process **(L26)** measures overall size.
Component 2 (male 9%, female 16%)	
Contrasts height of skull at base of mastoid **(L26)** with gnathion to anterior of foramen infraorbital **(L24)** and gnathion to posterior border of preorbital process **(L25)**.	Contrasts height of skull at base of mastoid **(L26)** with gnathion to anterior of foramen infraorbital **(L24)** and gnathion to posterior border of preorbital process **(L25)**.
Mandibular Component 1 (male 84%, female 70%)	
Length of mandible **(M28)**, height of mandible at meatus **(M31)** and angularis to coronoideus **(M32)** measure overall size.	Length of mandible **(M28)** and height of mandible at meatus **(M31)** measure overall size.
Component 2 (male 8%, female 21%)	
Contrasts height of mandible at meatus **(M31)** and angularis to coronoideus **(M32)** with others [length of mandible **(M28)**, length of mandibular tooth row **(M29)**, length of lower postcanine row **(M30)**].	Length of mandibular tooth row **(M29)** dominates.
Component 3 (male 5%, female 7%)	
Contrasts length of mandible **(M28)** with length of mandibular tooth row **(M29)** and height of mandible at meatus **(M31)**.	Contrasts length of mandible **(M28)** and length of lower postcanine row **(M30)** with height of mandible at meatus **(M31)** and angularis to coronoideus **(M30)**.

sex of tagged individuals would nearly always be known, as it would have been recorded when they were tagged.

We have focused on trying to develop a method for making an objective determination of sex based on only skull material. Aging untagged specimens from dentition (counting the growth layer groups in the upper canine) is an important component of making an objective sex determination.

The skull of an adult male ≥ 10 y is larger (**CBL** ≥ 248 mm; mastoid breadth ≥ 134 mm) and more robust than the skull of a similar aged female. In adult males, bony deposits occur throughout the parietal region of the skull, which become more prominent with increasing age (Rand, 1949ab; Stewardson et al., 2008; present study). Mean size of male sexually dimorphic traits, according to age (y), have been summarised elsewhere (Stewardson et al., 2008, 2009).

Classification and Regression Tree using 3 levels (58 animals)

Fig. 6 shows an animal is classified as being an immature male if **I25**<=73.7, **P12**<=35.85 and **P16**<=17.24 or if **I25**<=73.7, **P12**>35.85 and **M32**<=50.5 or if **I25**>73.7, **P12**<=45.1 and **D5**<=41.65. An animal is classified as being a mature female if **I25**<73.7, **P12**<=35.85 and **P16**>17.25 or if **I24**<=73.7, **P12**>35.85 and **M32**>50.5. An animal is classified as being a mature male if **I25**>73.7 and **P12**>45.1 or if **I25**>73.7, **P12**<=45.1 and **D5**>41.65. This rule correctly classifies 94.82% of the animals. Three immature males are misclassified as being a mature female (15% of all immature males). All mature females are correctly classified as being mature females, and all mature males are correctly classified as being mature females. Fig. 6 includes a prediction matrix to summarise the classification of the animals.

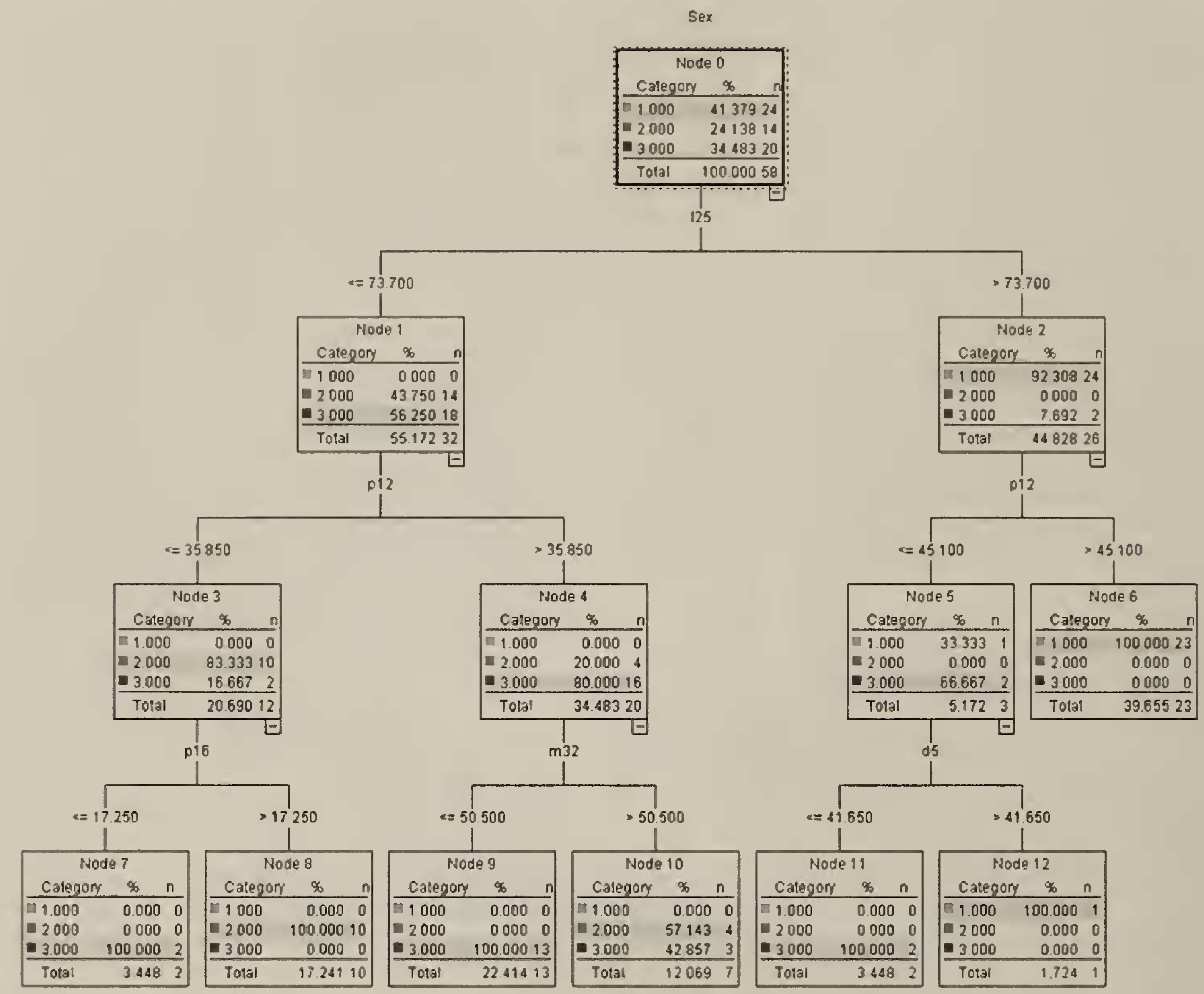
Hierarchical Cluster Analysis of skull parameters to produce a dendrogram (30 animals)

Cluster analysis was performed on thirty individuals where data on all variables were available, not counting **SBL** and sagittal crest height (**L27**). The observations were clustered using complete linkage (furthest neighbour) and Euclidean distance on all variables excluding **SBL** and **L27**. The four immature males lacking **SBL** data and hence for which there was some doubt about their actual sex (PEM 2006, 2009, 2010 & 2014) were excluded from the analysis. Cutting the dendrogram (Fig. 7) at a similarity level of 66.67 (or distance of 90) produces four clusters. The first cluster contains 2 males, 6 immature males and 2 females: PEM 975-M, PEM 2048-M, PEM 1014-F, PEM 1138-F, PEM 2046-IM, MCM 4577-IM, MCM 5133-IM, PEM 2050-IM, PEM 2052-IM, and PEM 2081-IM. The second cluster contains all males (10/10): PEM 1453-M, PEM 1892-M, PEM 2049-M, PEM 2051-M, PEM 2054-M, PEM 2087-M, PEM 2140-M, PEM 2141-M, PEM 2143-M, and PEM 2151-M. The third cluster contains 4 immature males and 3 females: PEM 2084-F, MCM 4578-F, MCM 5154-F, MCM 4595-IM, MCM 4996-IM, MCM 5002-IM, and MCM 5135-IM. The fourth cluster contains one female and 2 immature males: MCM 4994-F, MCM 4989-IM and MCM 5145-IM. Inclusion in the dendrogram of **SBL** data did not improve the ability to distinguish between immature males and females. Thus using cluster analysis it is easily possible to distinguish mature males from immature males and females but it is not possible to separate immature males from females.

DISCUSSION

Possible bias

Several factors must be taken into consideration when interpreting the data. Firstly, the sample size is small; in particular only 6 of the 14 females were aged. Secondly, there may be an over representation of either larger or smaller individuals in the data set which may possibly bias the results. Thirdly, although identical variables were taken from PEM and MCM animals, PEM variables were recorded by the first author, whereas MCM variables were recorded by the third author, introducing possible inter-observer error. However, the most likely source of bias is that some of the museum specimens identified as immature males may have been incorrectly sexed, especially if only the skull had been collected and the carcass had not been inspected properly, was badly decayed or was not available for examination. The results of the Classification and Regression Tree (Fig. 6) and the Cluster Analysis dendrogram (Fig. 7) emphasize that caution should be taken about the common claim that male and female skulls can be distinguished by visual inspection (Brunner 1998ab). The Classification and Regression Tree analysis was the more successful in correctly identifying the sex of the skulls. The cladistic dendrogram method had no difficulty in recognising mature male skulls but female and immature male skulls cannot be objectively separated from one another.



Prediction Matrix for 3-level Classification (n and %)			
Sex	Predicted Adult Male (1)	Predicted Female (2)	Predicted Immature Male (3)
Adult Male (1)	24 (100%)	0 (0%)	0 (0%)
Female (2)	0 (0%)	14 (100%)	0 (0%)
Immature Male (3)	0 (0%)	3 (15%)	17 (85%)

Fig. 6: Classification and Regressions Tree (CART) using three levels of skull data sets of adult male (M), immature male (IM) and female (F) South African fur seals (Total n = 58). A table is included to indicate successful and unsuccessful determinations of sex (M/F) and male reproductive status (IM/M). All the adult males (n = 24) were successfully identified as adult males. Three (3) immature males or 15% of the total (n = 20) were incorrectly classified as females but all the known females (n = 14) were correctly identified as females.

Principal component analysis: skull size and shape

For both genders, **CBL**, mastoid breadth, height of skull at base of mastoid, gnathion to posterior border of postglenoid process and length of mandible contributed the most to overall skull size (in multidimensional space). Gnathion to middle of occipital crest and basion to zygomatic root were predominant in males but not in females. Bizygomatic breadth was predominant in females but not in males.

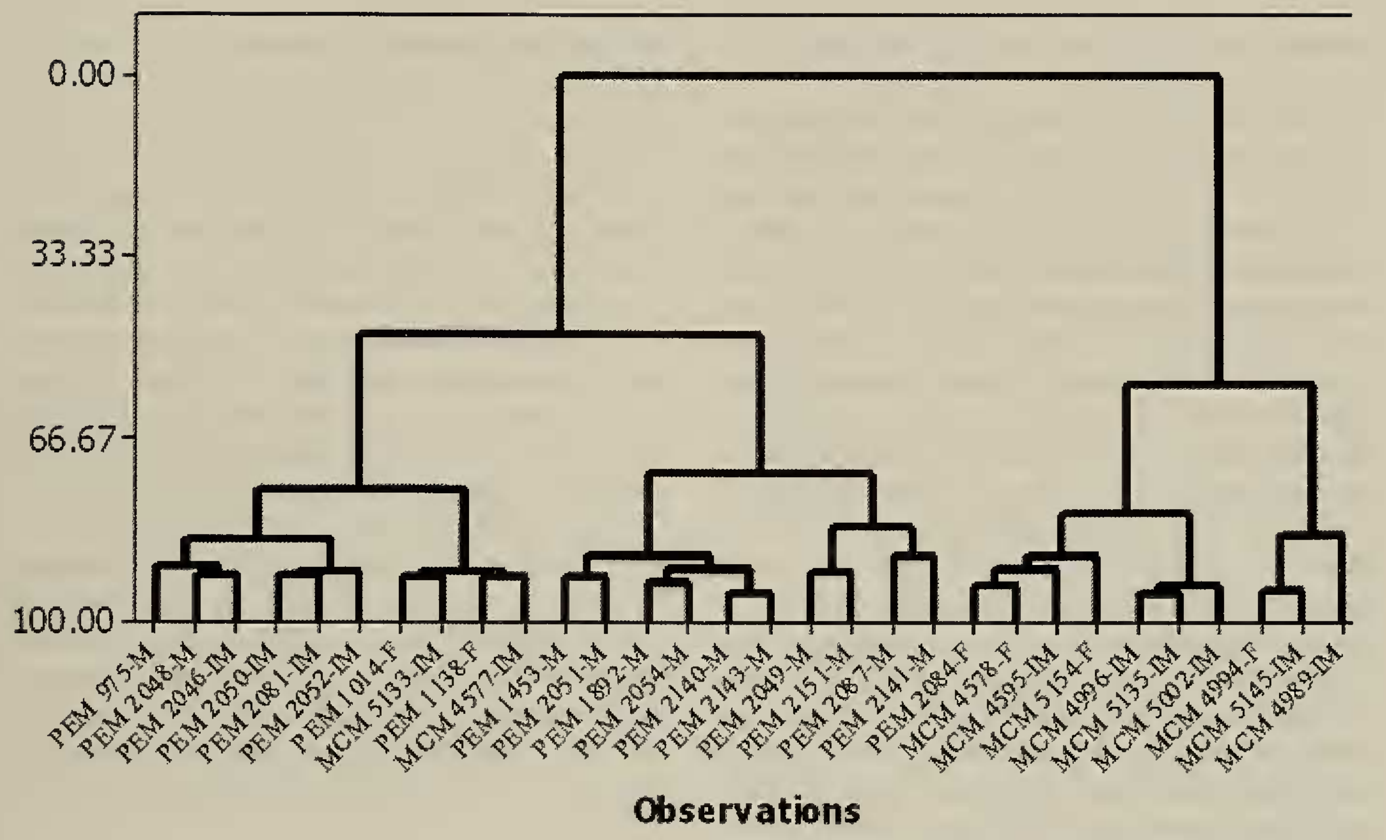


Fig. 7: Cladistic dendrogram based on complete sets of skull data for adult male (M), immature male (IM) and female (F) South African fur seals (Total n = 30). At the 66.67% similarity level the dendrogram divides into four groups or clades. One clade (#2) at the centre consists entirely of mature males (10/10) but the other three groups consist of two mature males (M), and a mixture of immature males (IM) and females (F). Clade (#1) consists of 2 females, 2 males and 6 immature males, clade (#3) consists of 3 females and 4 immature males and clade (#4) consists of 1 female and 2 immature males.

Predominant variables contributing to shape in both genders were **CBL**, breadth at supraorbital processes, breadth of brain case, palatal notch to incisors, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid, length of mandible, length of mandibular tooth row, length of lower postcanine row, height of mandible at meatus and angularis to coronoideus (see figures of South African fur seal skulls in Stewardson et al., 2008).

Bizygomatic breadth contributed predominantly to skull shape in males but not in females. Gnathion to posterior end of nasals, basion to zygomatic root and mastoid breadth contributed predominantly to skull shape in females but not in males.

These findings indicate that the underlying data structure for males and females was different. Differences occurred in the combination of predominant variables, and in their magnitude and sign.

General pattern of growth

Although male South African fur seals are slightly heavier than females (4.5 *vs.* 6.4 kg) at birth, growth patterns for the genders are reportedly similar up until puberty (Warneke and Shaughnessy, 1985). Males attain puberty between 3 and 4 y (Rand 1949b; Warneke and Shaughnessy, 1985; Stewardson et al., 1998) and females between 3 and 5 y (Rand 1949a; Warneke and Shaughnessy, 1985; Guinet et al., 1998, J.H.M David, pers. comm.).

Although males are sexually mature at an early age, they are physically unable to hold a harem until much later. Full reproductive status (social maturity) is deferred until full size and competitive vigour are developed. Males normally do not reach breeding or "beachmaster" status until about 10 y (Rand, 1949b; Stewardson et al., 1998). Some never attain breeding status. Females approximate adult size at about 5 y of age, while males attain adult size between 8 and 10 y (Rand, 1949a; Stewardson 2001; Stewardson et al., 2008, 2009). Adult males may weigh up to 353 kg (mean, 250 kg), while females may weigh up to 122 kg (mean, 58 kg) (David 1987; Guinet et al., 1998; J.H.M David, pers. comm.).

Redigitising the Australian fur seal data from Arnould and Warneke (2002), as described previously in our study of body size in male Australian and South African fur seals (Stewardson et al., 2009), it was possible to estimate the **SBL** of adult (>135 cm) female Australian fur seals to be 157 ± 0.758 (n = 144) cm. A two-sample t-test shows that Australian female fur seals were significantly larger than South African female fur seals ($p < 0.001$) but the overall difference is small (7.9 ± 2.6 cm). Guinet et al. (1998) based on adult females shot at a breeding colony in Namibia found the mean **SBL** of female South African fur seals to be 147 ± 0.56 cm (n = 157), which is not significantly different to that calculated in the present study (Appendix 3: 149 ± 2.49 cm, n = 18) . A two-sample t-test using their data, with its much larger sample size, leads to the same conclusion that female South African fur seals are slightly smaller than their Australian counterparts. These results are similar to the finding in male South African vs. Australian fur seals that the South African form of *Arctocephalus pusillus* is slightly smaller than the Australian variety (Stewardson et al., 2009). Overall then, both male and female South African fur seals are smaller than in the case of the Australian fur seal.

Studies of increase in **SBL** vs. age consistently show monophasic post-weaning growth patterns with different growth kinetics for each sex in the South African fur seal (Stewardson et al., 1998, 2008, 2009), Australian fur seal (Arnould and Warneke, 2002; Brunner et al., 2004; Stewardson et al., 2008, 2009) and other polygynous breeding pinnipeds which exhibit pronounced size dimorphism, e.g., Antarctic fur seal (*A. gazella*) and Southern fur seal (*A. tropicalis*) (Daneri et al., 2005), New Zealand fur seal (*A. australis forsteri*) (Brunner, 1998b; Brunner et al., 2004; McKenzie et al., 2007), Northern fur seals (*Callorhinus ursinus*) (McLaren, 1993) and the Steller sea lion (*Eumetopias jubatus*), based on several hundred individuals (Winship et al., 2001).

Development of the skull in male South African fur seals exhibits monophasic growth in some variables and biphasic growth in others (Stewardson et al., 2008, 2009). In males, biphasic growth in skull parameters is associated with reaching an age of about 8 to 10 y when some males attain full-breeding status (Stewardson et al., 2008). Similar growth patterns have been reported in the skulls of male New Zealand fur seals (Brunner, 1998ab; Brunner et al., 2004). There does not appear to be sufficient size/age data available to make statements about the growth dynamics of the female skull of any of the fur seal species.

Variation among adult males

The coefficient of variation for most skull variables was larger in males than in females (Stewardson et al., 2008; present study). Variability in adult males at least partly reflects differences in social status. Differences in physical appearance will be most noticeable before and during the breeding season when breeding bulls build up their body reserves. The specimens used in the present series of studies of South African fur seals (*A. pusillus pusillus*) (Stewardson et al., 2008, 2009) were based on fur seals collected from feeding areas on the eastern coast of South Africa rather than from breeding colonies and so would consist of a mixture of breeding and non-breeding animals. Data available on Australian fur seal (*A. pusillus doriferus*) are based on animals collected from breeding colonies (Arnould and Warneke, 2002; Brunner et al., 2004).

Loci of sexual dimorphism

Dorsal

Males were significantly larger than females ‘relative to **CBL**’ in four of the nine dorsal variables (gnathion to posterior end of nasals **(D3)**, breadth at preorbital processes **(D6)**, least interorbital constriction **(D7)**, breadth at supraorbital processes **(D8)**). In both genders, these variables form part of the splanchnocranium (gnathion to posterior end of nasals **(D3)**) and the frontal region (least interorbital constriction **(D7)** and breadth at supraorbital processes **(D8)**), and are associated with respiration/vocalisation (gnathion to posterior end of nasals **(D3)**) and feeding (breadth at supraorbital processes **(D8)**).

In males, at least two of these variables have obvious functional significance with respect to territorial acquisition and defence. Least interorbital constriction **(D7)** and breadth at supraorbital processes **(D8)** contribute to the structural strength of the skull, and shield the animal against blows to the head (especially the eyes) during combat with rival males. They also increase the width of the face of the seal, making it appear more intimidating to its rivals.

Palatal

Males were significantly larger than females ‘relative to **CBL**’ in five of the 14 palatal variables (greatest bicanine breadth **(P12)**, breadth of palate at postcanine 1 **(P15)** and postcanine 3 **(P16)**, calvarial breadth **(P21)** and mastoid breadth **(P22)**). In both genders, greatest bicanine breadth **(P12)**, breadth of palate at postcanine 1 **(P15)** and postcanine 3 **(P16)**, form part of the palatal region and are like other parameters from that part of the skull (greatest bicanine breadth **(P12)**, breadth of palate at postcanine 1 **(P15)** and postcanine 3 **(P15)**) are associated with feeding and respiration / vocalisation (greatest bicanine breadth). Calvarial breadth **(P21)** and mastoid breadth **(P22)** form part of the basicranium and are associated primarily with auditory function (calvarial breadth **(P21)**, mastoid breadth **(P22)**).

Enlargement of the canines (greatest bicanine breadth **(P12)**) enables males to inflict a potentially lethal bite during combat. The rostrum is broad (palatal breadth at postcanine 1 **(P15)** and postcanine 3 **(P16)**), accommodating the large canines. Enlargement of calvarial breadth **(P21)** and mastoid breadth **(P22)** increases intimidating size of the face and increases the structural strength of the skull (large head size/ mass).

Lateral

Males were significantly larger than females 'relative to **CBL**' in all lateral variables; that is, gnathion to anterior of foramen infraorbital **(L24)**, gnathion to hind border of preorbital process **(L25)** and height of skull at bottom of mastoid **(L26)**. In both genders, gnathion to foramen infraorbital **(L25)** and gnathion to hind border of preorbital process **(L25)** form part of the splanchnocranium and are associated with respiration/ vocalisation. Enlargement of skull height and facial length in males increases the overall head size.

Mandible

Males were significantly larger than females 'relative to **CBL**' in only one mandibular variable (height of mandible at meatus, **M31**). This variable is associated with auditory function and feeding in both genders (Stewardson et al., 2008). Enlargement of this variable in males increases gape and provides a larger surface area for muscle (masseter and temporalis) attachment. Large jaws and jaw muscles are advantageous in territorial combat.

Significance of the dimorphism

In male South African fur seals, there appears to be strong selection pressure for the development of certain morphological traits associated with fighting ability and body size and mass. It is important to note that beachmasters spend much of their time vocalising and intimidating rivals by displays which emphasise their size and the likely consequences of a rival attempting to challenge them rather than actual fighting (Rand, 1967; Stirling and Warneke, 1971; Miller, 1991). In male South African fur seals, selection pressure appears to favour large body mass. Stewardson et al. (2008, 2009) showed that males (mean, 183 cm) were significantly larger in standard body length than females (mean, 149 cm). Thus, on the mass/length cubed rule one would expect a male to weigh about 2 times that of an average female. Relative differences in body mass are much higher: large males in breeding condition may be 4-5 times heavier (average about 250 kg) than adult females, which average about 58 kg (David, 1989; Guinet et al., 1998; J.H.M David, pers. comm.). Large males have an advantage over their smaller rivals in gaining high social rank through vocalisation, intimidating display and fighting (Stirling and Warneke, 1971; Miller, 1991). Furthermore, large males in breeding condition have a well developed fat store. This thick blubber layer enables males to remain resident on territory for long periods (up to 40 days) without feeding and provides protection as well (Peterson, 1968; Alexander et al., 1979; McCann, 1981; Campagna and Le Boeuf, 1988; Boness, 1991). As in most seals, if for any reason a male abandons his territory, it will quickly be occupied by a rival male and the usurper will most likely have to be removed by actual combat (Rand, 1967; Le Boeuf, 1974; Miller, 1974; McCann, 1981; Campagna and Le Boeuf, 1988). There is a high risk of injury and/or failure in attempting to regain breeding territory.

Selection pressure also appears to favour the development of certain skull traits that appear to be associated with potential and actual fighting ability. In the present study, traits which are significantly larger in males appear to be associated with bite force (e.g., broad canines, increased surface area for muscle attachment, large gape), large head size/ mass (e.g., increased mastoid and calvarial breadth) and/or structural strength of the skull (protection against damage from direct blows to the head during combat).

Sexual dimorphism of the skull in southern fur seals has also been reported for the Australian and New Zealand fur seals (Australian fur seal, *A. pusillus doriferus* and New Zealand fur seal, *A. australis forsteri)* (Brunner, 1998ab). As with the South African fur seal, sexually dimorphic traits are mainly those characteristics that increase the ability of males to acquire and defend territory in the short breeding season whether by simply visually and vocally intimidating potential opponents or by actual combat (Bartholomew, 1970; Stewardson et al., 1998).

CONCLUSIONS

Information presented in the study demonstrates that there is pronounced sexual dimorphism in adult South African fur seals with respect to body length, body mass, skull size and skull shape. Male South African fur seals were significantly larger than females in **SBL**, and 43% of skull variables were found to be significantly larger in males relative to **CBL**. These variables were associated with fighting ability, e.g., large head size/mass, increased structural strength of the skull and/or increased bite capacity. Principal component analysis showed that the underlying data structure for males and females was different, and that most variation between the sexes was expressed in overall skull size rather than shape. This makes it generally easy to distinguish mature male and female skulls but problematic to distinguish skulls from sub-adult males from adult females. Condylobasal length **(CBL or D1)**, height of skull at bottom of mastoid **(L26)** and length of mandible **(M28)** contributed considerably to overall size, with gnathion to middle of occipital crest **(D2)** predominating in males only. Classification and Regression Tree analysis and cluster analysis dendrograms were both very successful for distinguishing mature male skulls from immature male and female skulls but Classification and Regression Tree was better than cluster analysis in distinguishing immature male from female skulls. The material used in the present study was from a feeding, not breeding area: it would be interesting to attempt to determine whether breeding bulls constitute an identifiable subset of the total adult male population some of which never breed.

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APPENDIX 1

Museum ascension numbers of male South African Fur seal specimens used in the present study. The data set of skull and body measurements on these specimens has been published previously in Stewardson et al. (2008). PEM stands for Post Elizabeth Museum (Port Elizabeth, South Africa), MCM stands for Marine and Coastal Management (Cape Town, South Africa).

The ascension numbers of the 39 adult male animals used in the present study were:
MCM 1809, MCM 4597, MCM 4992, PEM 898, PEM 951, PEM 958, PEM 975, PEM 1453, PEM 1507, PEM 1560, PEM 1587, PEM 1698, PEM 1868, PEM 1877, PEM 1879, PEM 1882, PEM 1890, PEM 1892, PEM 1895, PEM 2004, PEM 2007, PEM 2013, PEM 2036, PEM 2048, PEM 2049, PEM 2051, PEM 2052, PEM 2054, PEM 2082, PEM 2081, PEM 2087, PEM 2132, PEM 2140, PEM 2141, PEM 2143, PEM 2151, PEM 2248, PEM 2252, PEM 2258.

The skulls classed as immature (subadult) males (n = 24) were:
MCM 2763, MCM 2795, MCM 3582, MCM 3586, MCM 3587, MCM 3636, MCM 4365, MCM 4388, MCM 4577, MCM 4595, , MCM 4996, MCM 5002, MCM 5133, MCM 5135, MCM 5136, PEM 1704, PEM 1891, PEM 2006, PEM 2009, PEM 2010, PEM 2014, PEM 2046, PEM 2050, PEM 2053.

There were two (2) juvenile males only 2 years old:
MCM 4989, MCM 5145.

APPENDIX 2

Skull measurements and body measurements of female South African fur seals. SBL is standard body length (cm), all other parameters are coded as for Table 1 and are in mm.

Adults

Museum	Age	SBL	D1	D2	D3	D4	D5	D6	D7	D8	D9	P10	P11	P12	P13	P14	P15
number	y	cm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
PEM 918	-	144.0	204.5	172.3	72.8	-	40.1	52.4	28.3	40.0	80.0	78.6	55.1	33.1	93.4	11.0	18.8
PEM 929	-	160.0	222.8	190.7	75.4	-		52.3	28.0	44.3	96.3	94.0	55.8	41.0	100.2	14.0	22.4
PEM 931	-	150.0	212.6	184.9	71.4	-	34.8		29.0	44.8	79.0	72.9	59.6	38.7	99.0	12.0	17.4
PEM 957	-	150.0	215.9	184.3	74.0	23.6	39.2	58.4	29.6	42.9	81.8	90.9	56.1	37.8	102.6	14.0	20.5
PEM 1014	-	147.0	218.2	183.9	69.9	26.5	36.0	53.5	28.5	40.4	82.5	93.0	53.0	42.3	102.6	14.0	20.6
PEM 1133	-	155.0	225.0	190.7	79.6	24.8	42.4	-	31.9	46.5	82.1	94.8	55.8	44.0	105.6	13.0	20.5
PEM 1136	-	164.0	213.6	186.4	76.5	23.3	40.0	-	31.3	49.7	81.8	87.4	50.9	39.4	97.0	13.0	18.1
PEM 1138	-	142.0	216.3	190.1	78.5	23.3	41.4	56.3	31.6	47.1	83.8	85.5	58.4	38.5	102.7	12.0	19.2
PEM 1861	-	179.0	222.6	186.5	75.7	26.6	37.2	60.5	31.4	48.8	84.8	96.0	54.0	39.2	103.5	9.4	22.4
PEM 2084	-	145.0	208.3	181.2	71.3	21.0	36.4	50.3	28.8	44.1	79.3	89.1	56.6	35.2	98.0	12.0	17.4
MCM 101	-	148.0	217.6	187.2	73.5	26.9	38.9	57.6	31.9	50.3	82.3	92.4	57.5	39.6	100.8	13.1	19.9
MCM 1496	11.0	154.0	207.4	181.7	66.4	24.2	36.6	49.2	21.8	36.2	79.4	83.2	52.8	33.3	93.6	11.7	12.8
MCM 1551	12.0	145.0	201.5	178.3	69.3	25.0	33.9	52.0	24.2	-	82.9	83.4	53.9	35.4	93.6	10.4	19.4
MCM 1552	12.0	135.0	201.3	168.7	62.1	23.9	31.2	-	-	-	81.2	92.4	52.0	33.6	86.5	10.9	17.6
MCM 1556	12.0	143.5	209.2	179.9	71.2	24.8	37.6	50.7	21.5	43.2	79.8	91.2	55.5	35.8	98.9	11.3	18.8
MCM 4394	9.0	143.0	211.3	185.0	70.7	23.3	36.2	54.6	24.4	42.0	72.7	97.6	57.0	32.9	98.8	11.0	16.7
MCM 4578	-	145.0	210.2	179.1	74.8	21.1	38.6	49.3	22.8	39.3	84.4	85.7	55.0	32.3	98.1	13.0	16.9
MCM 5154	-	135.0	200.8	181.3	71.4	21.4	37.5	49.1	23.9	42.7	82.3	76.5	49.9	34.4	94.8	13.4	17.1

Museum	P16	P17	P18	P19	P20	P21	P22	P23	L24	L25	L26	L27	M28	M29	M30	M31	M32
number	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
PEM 918	21.2	29.1	152.0	108.1	140.0	93.3	104.7	68.9	57.4	64.5	85.9	-	141.3	56.1	40.5	41.6	48.0
PEM 929	24.1	30.4	163.0	118.4	154.0	95.3	105.2	73.7	61.1	66.1	93.7	-	155.0	60.6	42.8	49.0	51.0
PEM 931	19.0	26.0	164.0	118.6	144.0	97.6	113.2	66.3	60.0	66.6	92.2	-	156.1	48.6	47.6	47.8	48.0
PEM 957	20.6	26.3	162.0	127.4	146.0	104.0	113.3	70.0	-	-		-	-	-	-	-	-
PEM 1014	20.7	25.5	164.0	123.6	147.0	99.3	110.7	68.4	63.5	68.3	91.6	-	154.0	62.5	44.0	48.5	52.0
PEM 1133	-	27.6	170.0	132.8	156.0	102.0	115.8	73.3	64.0	69.4	92.2	-	160.7	64.3	44.5	49.8	53.0
PEM 1136	20.1	26.5	163.0	122.8	144.0	96.7	112.2	68.9	63.7	70.8	91.2	-	150.0	42.5	26.3	46.1	49.0
PEM 1138	22.8	27.7	163.0	131.9	149.0	98.6	114.1	73.1	63.5	69.6	92.6	-	148.0	53.0	40.7	47.6	51.0
PEM 1861	22.4	24.4	166.0	126.0	153.0	95.3	113.2	73.6	62.5		91.7	-	150.7	43.3	43.7	41.0	44.0
PEM 2084	19.6	24.6	156.0	119.0	140.0	92.9	103.3	66.3	61.3	67.7	82.3	-	147.1	60.3	44.1	42.7	44.0
MCM 101	21.2	29.1	165.3	132.1	149.7	98.3	116.2	70.9	71.1	69.6	-	5.1	151.2	53.0	42.3	49.4	51.3
MCM 1496	21.4	27.0	155.8	116.4	144.8	92.9	106.4	70.5	57.2	62.7	-	0.3	141.9	57.7	43.2	39.1	44.9
MCM 1551	23.1	29.3	151.9	113.6	143.3	90.4	97.3	67.3	57.2	60.8	-	-	135.3	55.3	41.2	41.3	43.5
MCM 1552	20.0	24.0	148.4	110.2	140.4	89.5	98.6	68.2	50.5	58.9	-	0.0	135.8	53.7	39.2	42.0	48.3
MCM 1556	22.6	29.0	157.9	117.5	143.0	94.4	106.3	64.9	56.7	63.3	-	-	143.7	57.8	42.4	42.0	47.1
MCM 4394	20.2	27.8	153.8	114.0	141.6	93.4	102.0	72.3	62.0	66.2	-	0.0	141.2	59.0	43.0	40.7	43.2
MCM 4578	20.6	24.7	157.9	119.4	146.9	91.8	100.2	66.6	62.6	65.2	80.8	0.1	141.5	54.4	39.9	39.7	42.7
MCM 5154	19.6	22.9	148.7	109.1	136.9	87.4	102.6	66.4	58.5	63.2	81.3	0.0	132.5	55.8	40.3	40.7	43.5

Juveniles/Subadults

Museum	Age	SBL	D1	D2	D3	D4	D5	D6	D7	D8	D9	P10	P11	P12	P13	P14	P15
number	y	cm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
MCM 1802	2.9	116.0	182.0	154.9	58.4	20.8	28.5	48.2	24.8	37.5	81.1	74.8	46.9	29.7	84.6	11.9	15.4
MCM 4990	1.8	83.0	152.7	132.3	51.7	18.1	24.5	40.2	20.4	36.2	77.4	61.4	41.0	28.8	69.7	10.0	12.9
MCM 4994	1.8	90.0	163.7	144.7	47.3	16.9	21.1	42.4	20.2	34.9	76.2	71.4	42.4	27.6	72.3	10.6	12.0

Museum	P16	P17	P18	P19	P20	P21	P22	P23	L24	L25	L26	L27	M28	M29	M30	M31	M32
number	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
MCM 1802	18.0	21.4	132.2	103.7	125.4	82.0	89.3	64.5	50.0	57.0		0.0	120.3	50.7	38.2	32.2	33.9
MCM 4990	17.5	20.7	108.9	85.5	107.5	71.2	66.3	54.6	39.6	45.7		0.0	98.3	44.0	31.7	25.3	29.3
MCM 4994	18.3	20.7	116.6	87.4	115.2	75.3	78.8	60.5	41.8	47.1	69.2	0.0	103.7	45.1	33.2	22.1	30.0

APPENDIX 3.

Numbers of Individuals, Means, Standard deviations, Standard Errors and ranges of Standard Body length (SBL) and Skull Measurements in Female South African fur seals.

	SBL	D1	D2	D3	D4	D5	D6	D7	D8	D9	P10	P11	P12	P13	P14	P15
Units	cm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
Count (n)	18.00	18.00	18.00	18.00	15.00	17.00	14.00	17.00	16.00	18.00	18.00	18.00	18.00	18.00	18.00	18.00
Mean	149.14	212.17	182.90	72.47	23.98	37.53	53.30	26.99	43.89	82.02	88.03	54.94	37.03	98.32	12.18	18.69
SD	10.55	7.50	5.91	4.21	1.88	2.79	3.69	5.21	3.92	4.48	6.97	2.56	3.51	4.66	1.34	2.29
SE	2.49	1.77	1.39	0.99	0.49	0.68	0.99	1.26	0.98	1.06	1.64	0.60	0.83	1.10	0.32	0.54
Maximum	179.00	225.00	190.70	79.60	26.90	42.40	60.50	31.90	50.30	96.30	97.60	59.60	44.00	105.60	14.00	22.40
Minimum	135.00	200.80	168.70	62.10	21.00	31.20	49.10	11.50	36.20	72.70	72.90	49.90	32.30	86.50	9.40	12.80

	P16	P17	P18	P19	P20	P21	P22	P23	L24	L25	L26	L27	M28	M29	M30	M31	M32
Units	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
Count	17.00	18.00	18.00	18.00	18.00	18.00	18.00	18.00	17.00	16.00	11.00	6.00	17.00	17.00	17.00	17.00	17.00
Mean	21.13	26.77	159.04	120.05	145.53	95.17	107.52	69.42	60.75	65.81	88.68	0.92	146.24	55.17	41.51	44.06	47.32
SD	1.43	2.14	6.34	7.75	5.23	4.31	6.15	2.88	4.43	3.41	5.04	2.05	7.99	6.02	4.43	3.84	3.51
SE	0.35	0.50	1.49	1.83	1.23	1.02	1.45	0.68	1.07	0.85	1.52	0.84	1.94	1.46	1.08	0.93	0.85
Maximum	24.10	30.40	170.00	132.80	156.00	104.00	116.20	73.70	71.10	70.80	93.70	5.10	160.70	64.30	47.60	49.80	53.00
Minimum	19.00	22.90	148.40	108.10	136.90	87.40	97.30	64.90	50.50	58.90	80.80	0.00	132.50	42.50	26.30	39.10	42.70